Pistillate inflorescences (Fig. 7) have fewer, commonly shorter branches than staminate, with flowers more widely spaced (1–2 mm. apart). In staminate inflorescences (Fig. 1), third order branches are more common, often longer, and flowers are more crowded (0.5–1 mm. apart), sometimes opposite, or in pairs. Many more flowers are produced in a staminate than in a pistillate inflorescence (Table 1).

Anatomy. Anatomically all rachillae are similar. Epidermal cells are small with rounded to slightly papillose outer walls. A thin cuticle is present. The cortex is moderately wide and of unspecialized parenchyma cells which increase in diameter centripetally. Some of the cells contain tannins. The vascular complement consists of both large and small bundles. Each larger bundle has one or two large vessels, a single phloem strand, and a fibrous sheath four to five cells wide next to the phloem and two to three cells wide next to the xylem. Smaller bundles have fewer vascular elements; a few may contain only a phloem strand or be completely fibrous. In general these axes differ from the main axis in having less lignified ground tissue and fewer cortical fibrous strands.

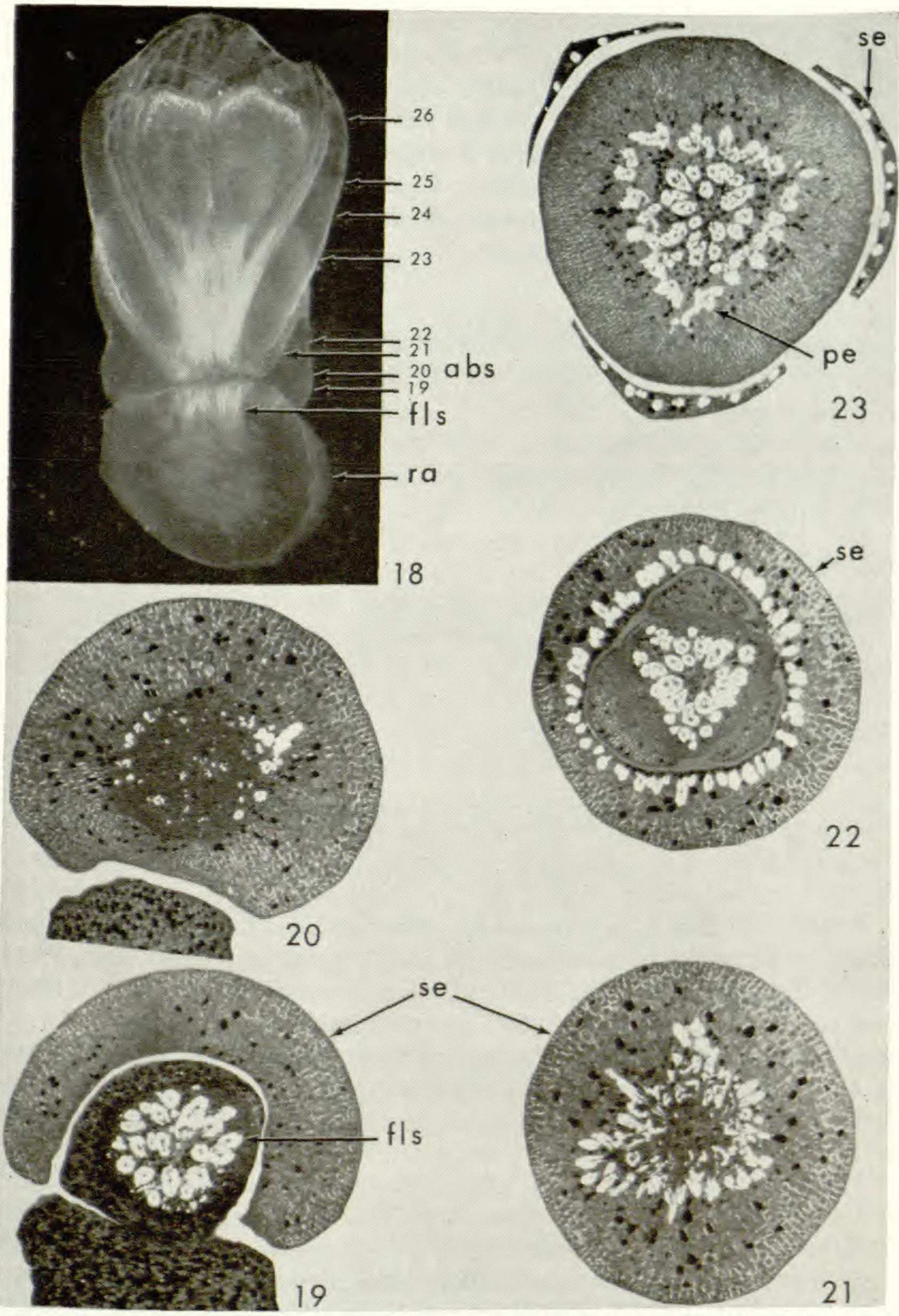
There is a definite arrangement and orientation of axial bundles in rachillae of many palms. In *Rhapis*, a transection of a rachilla at any level shows some large central bundles, one or two peripheral groups of smaller bundles, and some scattered fibrous or very small vascular bundles in the inner cortex. This configuration is easily explained in terms of

origin of bundles to the flowers.

Slightly below and opposite a floral insertion, six to ten axis bundles branch (Fig. 18, fls) to form the bundles supplying the flower. A single axial strand may produce one to four small branches in close vertical succession or in a horizontal plane. Commonly the vertical derivative continues as an axial bundle; however all branches of a bundle may become floral traces. The peripheral clusters of small bundles are traces to higher flowers; consequently, the number of small bundles varies depending on the proximity to a floral insertion.

One or two axis bundles as well as branches from many others extend directly into each flower. The total number of bundles in a rachilla is thus progressively reduced distally (Table 1). Bundles in the axis branch frequently, providing the numerous traces to flowers. Absolute numbers of bundles are difficult to determine because bundles branch frequently, the levels at which bundles are counted cannot be considered perfectly comparable, and fibrous sheaths of main strands and branches are often confluent. Mere vigor or order of the branch may also affect the number of bundles in a rachilla. However, the number of bundles in floral stalks and organs seems to vary within definite limits. Approximately 6 to 9 bundles are present in staminate floral stalks below the abscission zone, and a larger number (20–25) in pistillate floral stalks.

Rachillae are not terminated by flowers. In pistillate branches a rounded or pointed projection of the axis extends beyond the flower; some 14 to 16 vascular bundles are present in this reduced tip. Staminate



Figs. 18-23. Pistillate flower. Fig. 18, cleared half of a pistillate flower, × 10; levels of succeeding figures (19-26) indicated by the appropriate numbers; Fig. 19, transection of the floral stalk, × 18, level 19 in Fig. 18; Fig. 20, transection through abscission zone, × 18; Fig. 21, transection at level of origin of sepal traces, × 18; Fig. 22, transection at level of origin of petal traces, × 18; Fig. 23, transection showing distal parts of sepals, petal traces form outer triangular group of bundles, × 18. Details: abs, abscission zone; fls, floral stalk; pe, petal traces; se, sepal; ra, rachilla.

rachillae usually end less abruptly, one to seven abortive flowers being present. Bracts subtending these abortive flowers are more prominent than bracts of normal flowers, which are often obscured as the axis and flower increase in size. A difference in growth patterns is suggested in the two types of inflorescences. More branches and more flowers per branch are formed in staminate inflorescences, suggesting that factors affecting branch and floral initiation are more active and that cessation of growth is less abrupt.

TABLE I. Flowers and Bundles per cm. of Length in Rachillae

1 cm. intervals, base to apex	Pistillate rachilla		Staminate rachilla	
	bundles/cm.	flowers/cm.	bundles/cm.	flowers/cm.
base	50		42	
1	43	4	36	3
2	40	5	35	7
3	40	4	35	10
4	39	4	31	9
5	31	3	28	15
6	16	1	28	12
7	16		26	13
9			19	14
10			12	13
11			5	7 abortiv

PISTILLATE FLOWER

Bracts. Each pistillate flower is subtended by a bractlet (Fig. 7, br). Bractlets subtending basal flowers on rachillae may be larger than bractlets of distal flowers which are usually small, crowded between the flower and the axis, and apparent only when flowers are detached (Fig. 7). A small trace, originating as a branch of an axis bundle, is usually present in the bractlet. One or more floral traces may originate from the same stelar bundle from which the trace to the bractlet diverged at a lower level.

Morphology (Figs. 7–17). Although considerable connation and adnation are present in floral organs, a 3–3–6–3 floral plan is obvious both morphologically and anatomically. Sepals of pistillate flowers (Figs. 8, 9, 10) are connate forming a shallow parenchymatous cup about 1 mm. high with three pointed lobes 1–1.5 mm. long. The three petals (Fig. 11) are also connate for approximately 3 mm., above which the free lobes are briefly imbricate and then valvate reaching an additional length of 1–2 mm. The staminodes (Fig. 12) resemble the stamens in staminate flowers but are smaller. The filaments are linear, adnate to the petal tube for 1 mm., and free above that for about 0.5 mm. In the material studied the reduced anthers did not produce pollen.

The three separate carpels (Fig. 13) are wedge-shaped with flat ventral sides and rounded and grooved dorsal sides (Figs. 13, 16). Each carpel has a distinct stalk which is fused with the petal-staminode tube for a very short distance basally (Fig. 24). A locule with a single basal ovule occupies the lower half of the carpel (Figs. 12, 14). Distally the style is wide; the upper part is distended abaxially and converges abruptly toward the ventrally situated, conduplicate, tube-shaped stigma (Fig. 28). Thus the styles of these carpels are enlarged and are also histologically specialized, as described below.

A single, hemianatropous ovule with a large funicular aril is attached basally in the ventral angle of the locule (Fig. 27). There are two integuments which are free for about 1/3 the length of the ovule. The outer integument is six to seven cells wide and increases to about nine cell layers around the micropyle. The inner integument consists of two cell layers and is widened to three to four cells around the micropyle to form a short beak. The inner layer of the inner integument is specialized as an integumentary tapetum.

Anatomy (Figs. 18–32). Pistillate flowers appear to be sessile (Fig. 7). Anatomically, however, a very short stalk with a distinct group of floral traces, can be recognized (Fig. 19). As explained above, the majority of the bundles of the floral axis originate as branches from strands in the rachilla, one or two of which also extend directly into the flower without branching. The number of bundles supplying the pistillate flower (Fig. 19) is about 23

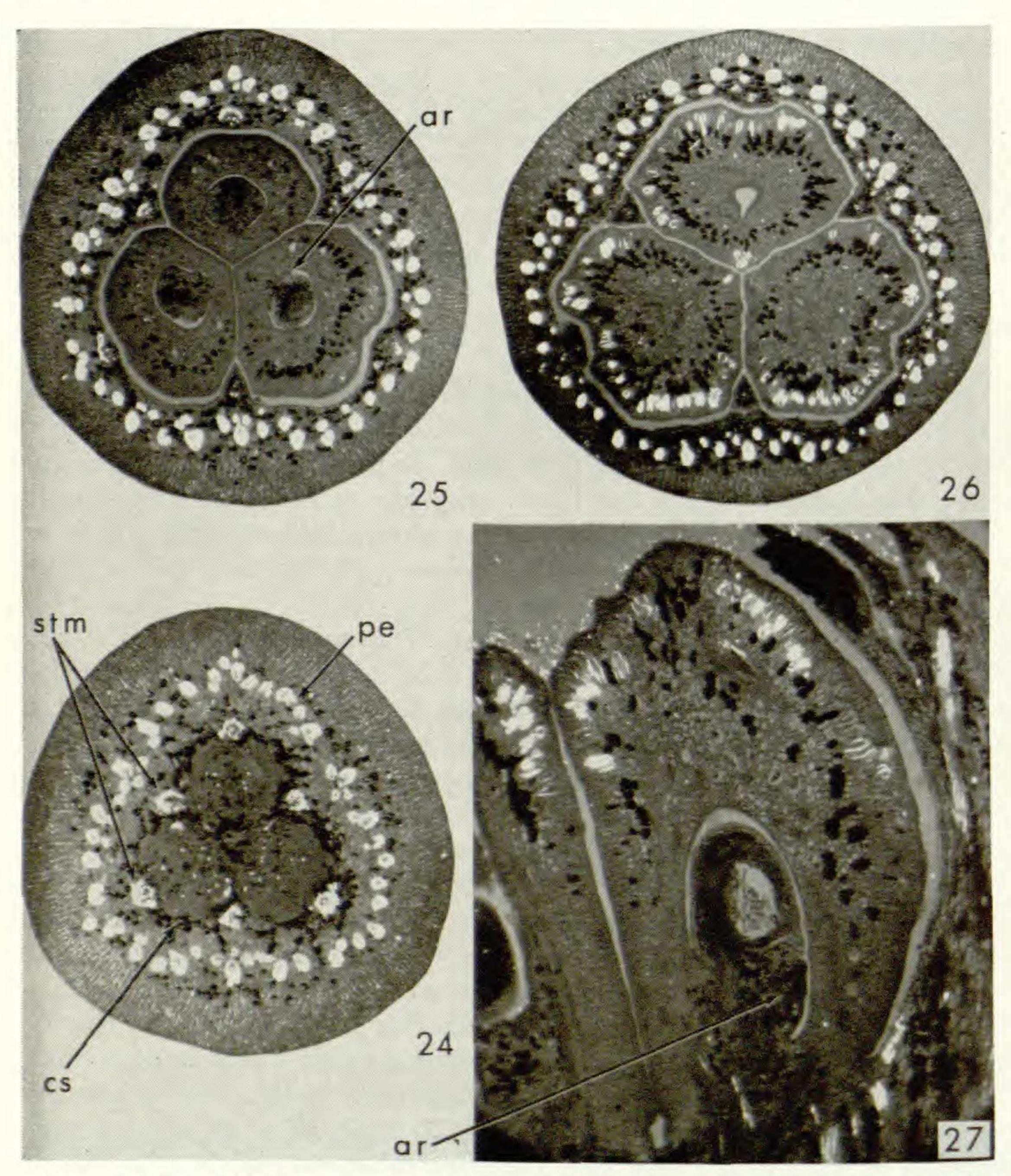
An abscission zone forms a characteristic feature of floral stalks of both staminate and pistillate flowers (Fig. 18, abs). This zone is distinguished by the absence of fibrous bundle sheaths and by smaller ground paren-

chyma cells (Fig. 20) through which bundles can be followed.

Generally, in palm flowers, even when organs are connate, the origin of their traces indicates a spiral insertion. This is not apparent in the sepals or petals of *Rhapis*. Directly above the abscission zone, most bundles of the floral axis branch at about the same level (Fig. 21) to form about 30 sepal traces. The origin and horizontal divergence of so many bundles at one level results in a collar-like complex in which inner bundles extend radially between outer strands and some lateral fusion of bundles occurs (Fig. 21). Individual bundles may be followed through this complex. Figure 38 is a radial plot of a single major bundle of the floral axis. The sepal trace (se 1) originating from this bundle branches to form three other sepal traces (Fig. 39, se 2, se 3, se 4) and these bundles in turn branch forming the continuing vertical bundles VB 2, VB 3, and VB 4. Smaller (minor) bundles of the floral axis may produce only a single sepal trace or extend directly into the sepal.

Above the sepal complex about 30 vertical bundles form a central group (Fig. 22). Some 30 to 40 petal traces diverge at an acute upward angle (30° to 40°) from these as opposed to a near 90° angle of divergence for sepal traces (Fig. 18). Smaller vertical bundles (Fig. 39, VB 2 and

VB 3) may extend directly into a petal without branching. Most petal traces, at the level of their origin, contain phloem only and fibrous sheaths of main bundles and branches are often confluent (Fig. 23, pe). At higher levels where traces are separate, a few scalariform xylem elements are present. Sclerenchymatic sheaths of petal traces are thinner walled than those of sepal traces. As in the sepals, a few lateral bundles may branch and a median and two lateral veins extend into each petal tip.



Figs. 24-27. Pistillate flower, continued. Fig. 24, transection through stalks of the three carpels, outer ring of bundles are petal traces, inner six large bundles supply staminodes, all bundles in carpel bases are provascular, × 18; Fig. 25, transection through petal-staminode tube and three carpels at level of funicular attachments, × 18; Fig. 26, transection showing petal-staminode tube and expanded styles of carpels, × 18; Fig. 27, longitudinal section of one carpel, × 35. Details: ar, aril; cs, carpel stipe; pe, petal trace; stm, staminode trace.

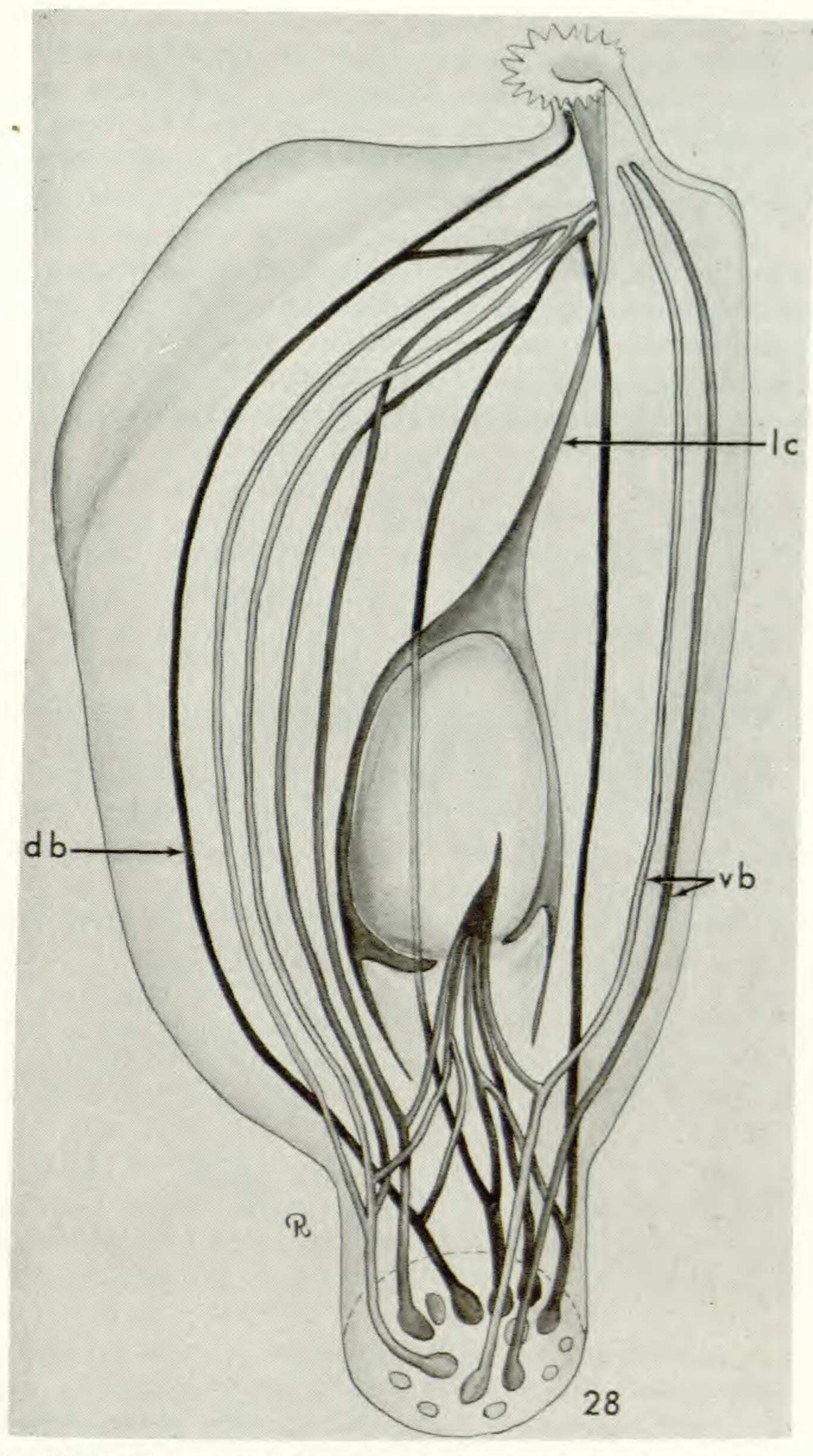
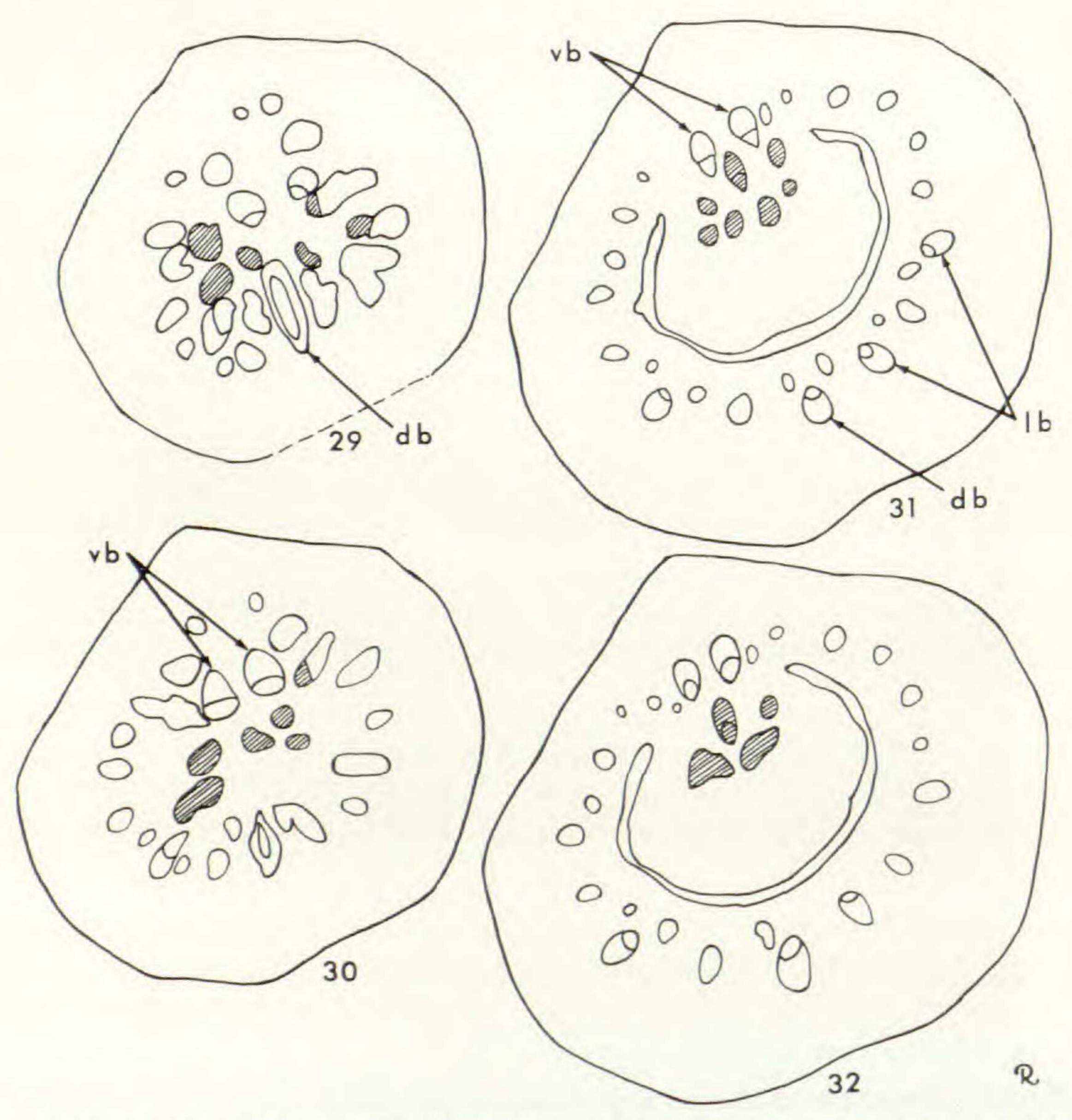


Fig. 28. Three dimensional drawing of one carpel to show vascular supply. Dorsal and ventral bundles labeled, remaining are lateral bundles. Seven lateral bundles are not completed for clarity, × ca. 50. For details see Figs. 29–32.

About 20 relatively large receptacular bundles, each with a complete fibrous sheath (Fig. 23, central bundles) are present above the origin of the petal traces. Just above this level, considerable reorientation and

branching of strands takes place. Traces to staminodes (Fig. 24, stm) are formed, often as a central branch of a trifurcating receptacular bundle. Traces to antisepalous staminodes diverge at a slightly lower level than those to the antipetalous ones. The remaining bundles become oriented into three groups, one group representing the supply to each carpel.

Fibrous bundle sheaths extend as far as the stalk of each carpel but are absent in the carpel base where all bundles are procambial. Three or four of the bundles in each carpel base are larger than the remainder and possess xylem elements which are birefringent. The central of these larger strands extends across the carpel base and distally around the locule to the base of the stigma (Fig. 28, db). Two of the other larger strands remain in ventral positions (Figs. 28, 29–32, vb). Thus a dorsal



Figs. 29-32. Series of transections through the base of one carpel drawn with Wild M20 research microscope and drawing tube, to show origin of ovular supply. Ovule traces shaded, bundles with birefringent xylem shown divided, × 60. Details: db, dorsal bundle; lb, lateral bundle; lc, locular canal; vb, ventral bundle.

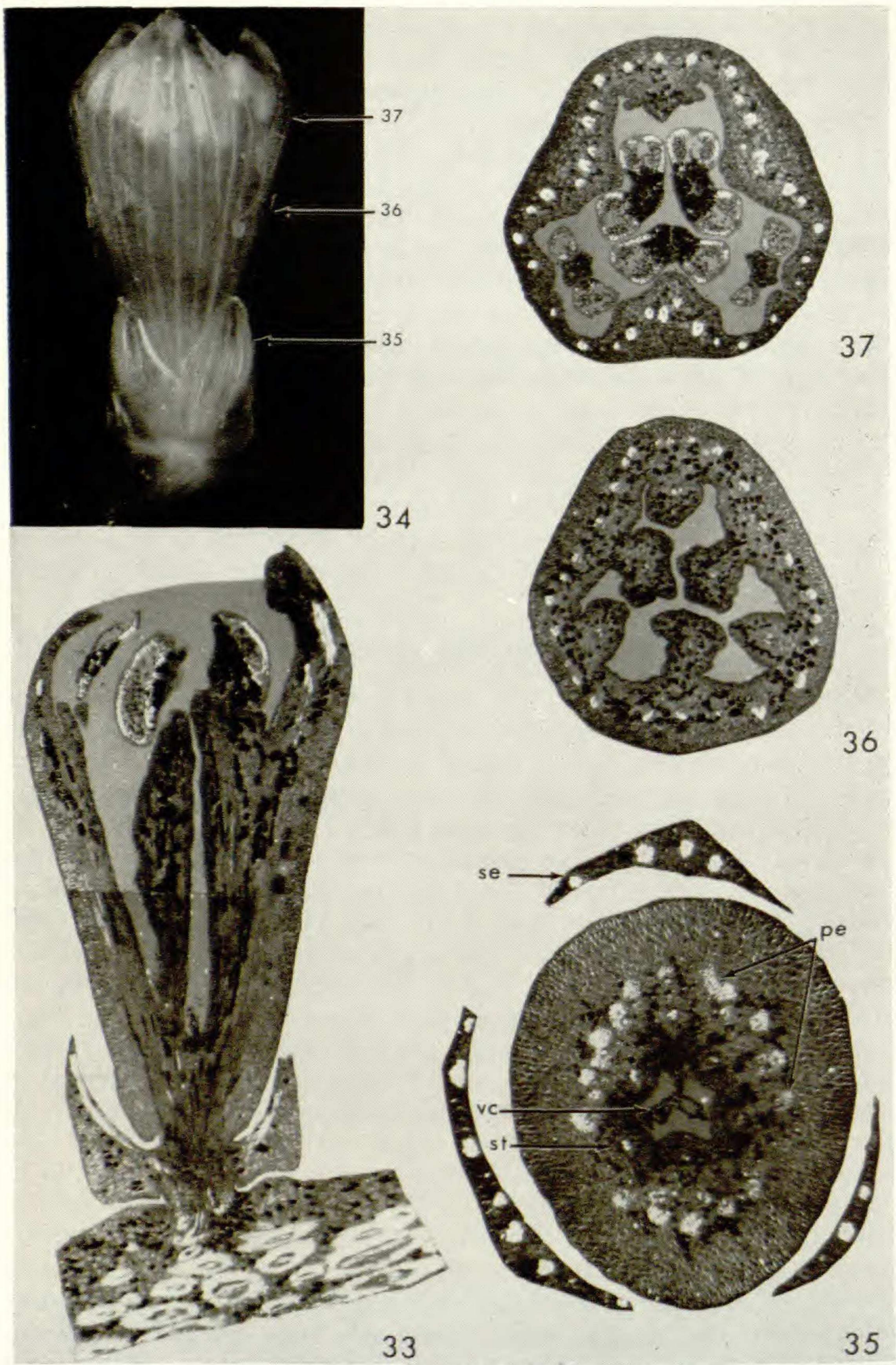
and two ventral bundles can be recognized by size, position, and maturity (Figs. 29–32). Remaining strands form the 20 to 24 lateral bundles present in an irregular ring in the carpel wall (Figs. 31, 32). Four of these are larger and more mature (Figs. 31, 32, lb). Some lateral bundles fuse with others near their upper limits, the major ones extending toward the locular canal (Fig. 28). The ventrals extend slightly higher and the dorsal ends just below the stigma (Fig. 28).

The origin of the vascular supply to ovules varies in palms (Uhl, unpublished). In *Rhapis*, a branch from the dorsal bundle, a branch from each of four or five lateral bundles, and a branch from one ventral bundle form a group of strands (Figs. 29–32) which extends into the funiculus (Fig. 28). These strands fuse near the chalaza and the resulting large bundle ends near the base of the outer integument. A similar pattern for the origin of ovule traces has been observed in *Trachycarpus* and *Corypha*. Angiosperm taxa with more than one trace to the ovule and with traces derived from dorsal and ventral carpellary bundles are not frequent. Such taxa occur in groups usually considered to be primitive, as Magnoliaceae (Canright, 1960) and Nymphaeaceae (Moseley, 1961).

STAMINATE FLOWER

Morphology (Figs. 1-6). A comparison of staminate and pistillate flowers shows both differences and similarities. Bractlets are alike in both types of inflorescence. Sepals in the two flowers (Figs. 3, 4) are also similar in shape and size; those of staminate flowers are perhaps slightly less fleshy. Petals are about the same length (4-5 mm.) and are 2/3 to 3/4 connate (Figs. 3, 5). In staminate flowers, however, the petal tube is definitely obovoid or clavate and much less fleshy than that in pistillate flowers (cf. Figs. 8 and 11 with 3 and 5). The diameter of the petal tube immediately below the free lobes is approximately 2 mm. in staminate flowers and 3 mm. in pistillate flowers. Staminate petals are valvate and often incompletely connate, a groove of varying depths showing the limits of each petal. In pistillate flowers, however, the petal-tube is smooth and free lobes are briefly imbricate. Filaments (Fig. 6) are wider in stamens than in staminodes and bear well-developed, latrorse anthers with dark, tannin-containing connectives (Figs. 33, 37). Three very tiny vestigial carpels are present (Figs. 33, 35, vc).

Anatomy (Figs. 33-37). The origin of traces to floral organs is similar to that described for pistillate flowers except that in some organs fewer bundles are present. The number of traces to sepals is approximately six to eight (Figs. 34, 35). Petals receive only three, four, or five bundles (Fig. 35) as opposed to eight to ten in pistillate flowers. Major petal traces also branch more frequently in pistillate flowers. Thus there are many more bundles in petals of pistillate than in those of staminate flowers (cf. Figs. 25 and 26 with 36 and 37). The traces to stamens originate in two groups of three and are large, sometimes double vascular



Figs. 33-37. Staminate flower. Fig. 33, longitudinal section, × 18; Fig. 34, cleared staminate flower, levels of figures 35-37 indicated by the appropriate numbers, × 10; Fig. 35, transection through base of flower, × 35; Fig. 36, transection through petal-stamen tube, × 18; Fig. 37, transection of distal part of flower, ×18. Details: pe, petal traces; se, sepal; st, stamen trace; vc, vestigial carpel.

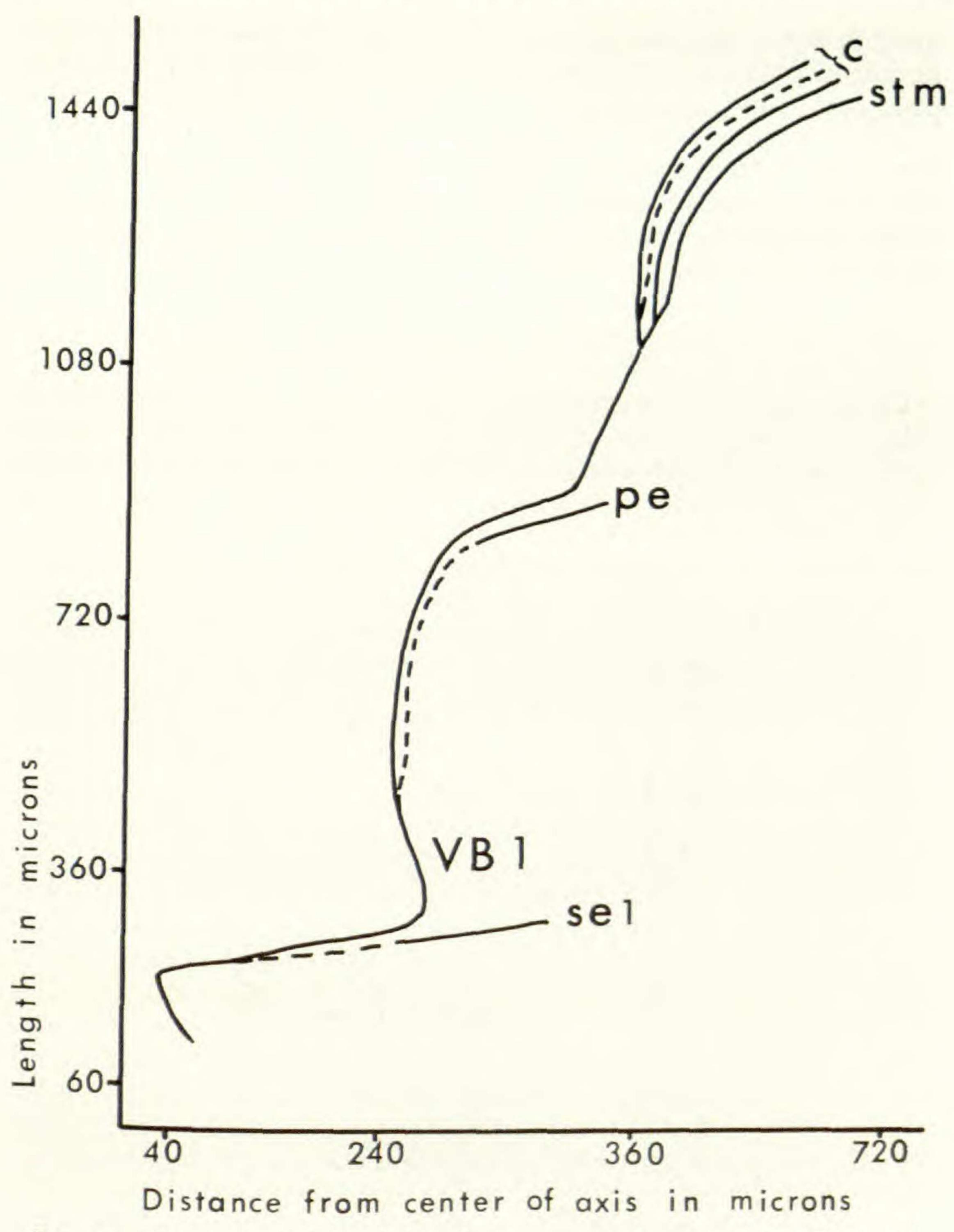


Fig. 38. Diagram of the radial path of a major bundle of the floral axis. Details: c, carpel traces; pe, petal trace; se, sepal trace; stm, staminode trace; VB 1, continuing vertical bundle. Dotted lines indicate where fibrous bundle sheaths are confluent.

bundles. About three strands remain in the floral receptacle above the origin of the stamen traces. These disappear just below the vestigial carpels.

Histology. Histological features in floral organs are sometimes diagnostic in palms (Uhl, unpublished). In Rhapis, tannins are present ran-

domly in sepals and filaments, near the adaxial surfaces of petals and in all cells of connectives. Fibrous bundle caps are lacking in receptacular, lower petal, and stamen bundles of staminate flowers; in carpels; and in abscission zones of both flowers. It is perhaps significant that there are few, if any, crystals in fleshy sepal bases and petal tubes. The abaxially distended styles are histologically the most specialized parts of the flowers, containing raphides, tannin cells in radial rows, and distal, cap-like layers of sclereids (Fig. 26).

DISCUSSION

Comparison with vegetative organs. Emphasis in this series on Rhapis has been on vascular pathways throughout the plant. Careful analysis of the flowers shows continuity of bundles from those of the

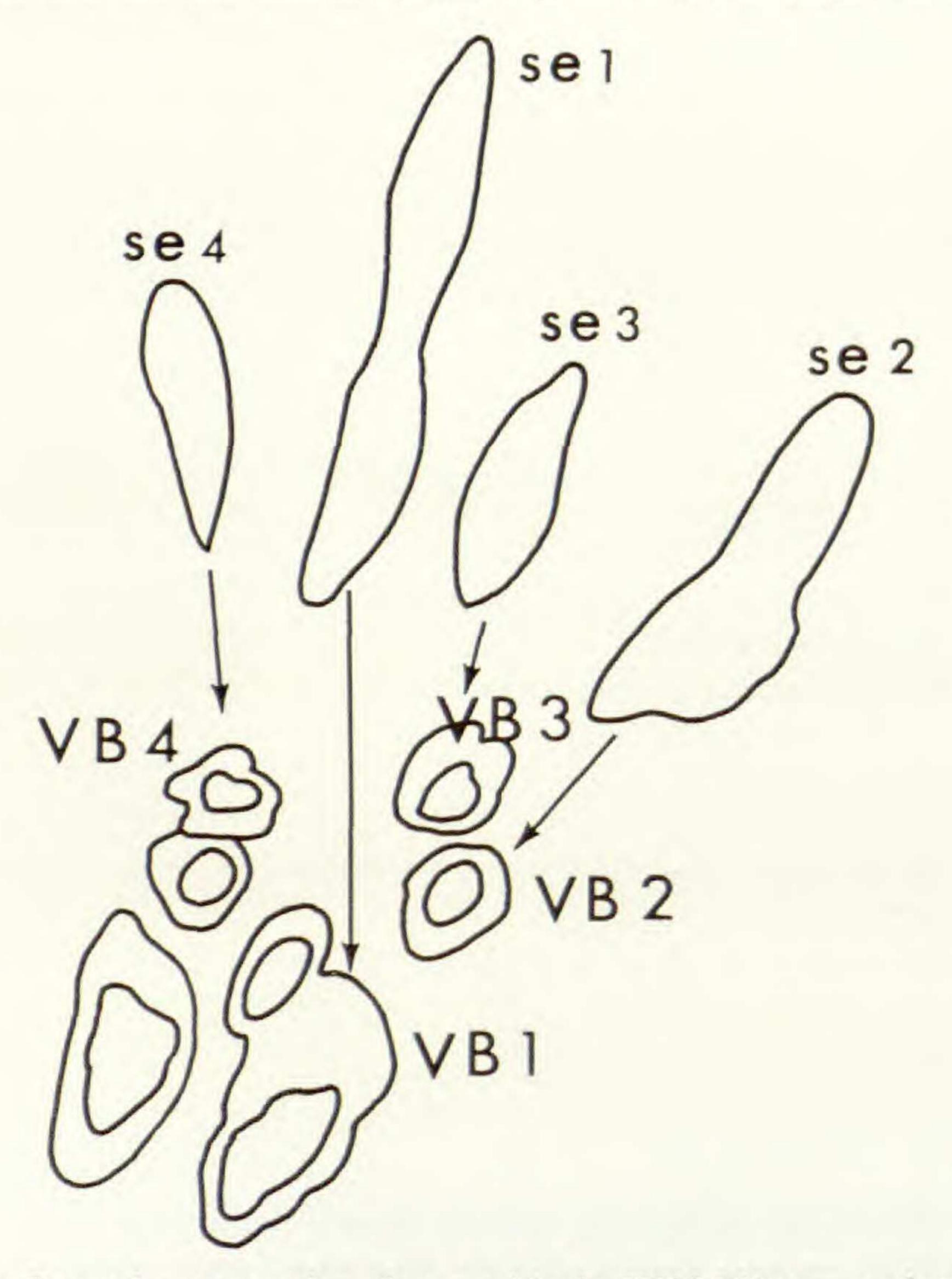


Fig. 39. Part of a transection, drawn with the Wild M20 research microscope and drawing tube, to show the continuation of the sepal trace (se 1) diagrammed in Fig. 38; se 2, se 3, and se 4 are sepal traces derived as branches of se 1. Each of these branches to form a continuing vertical bundle (VB 2, VB 3, and VB 4) as indicated, × 125.

rachilla to the ovule or stamen. The pattern of origin is a simple one. Bundles of the floral axis, derived as branches of rachilla bundles, branch in turn at appropriate levels to provide traces to sepals, petals, staminodes or stamens, and carpels.

This vascular continuity throughout Rhapis, which is now completed in the description of floral vasculature, shows a similar pattern throughout every kind of axis on the plant (e.g. seedling, aërial axis, rhizome, inflorescence axis, rachilla, and pedicel). The same principle of vascular organization is expressed in the flower, but it is somewhat more difficult to recognize here than in the vegetative organs because the floral axis is condensed and the lateral organs are small. Nevertheless we may say that the divergence of traces to sepals, petals, and staminodes or stamens, involving axial continuity, is comparable to the departure of leaf traces in rhizome and aërial stem (Tomlinson & Zimmermann, 1966; Zimmermann & Tomlinson, 1965). This is most obvious when an individual bundle is followed through the floral axis. The radial path resulting from such an analysis is presented diagrammatically in Figure 38. In addition very short bundles, which may be interpreted as bridges (Zimmermann & Tomlinson, 1965), often link diverging traces with bundles of the receptacular system. More detailed comparison of floral and vegetative vascular pathways must await a more complete understanding of monocotyledonous vascular development.

Comparison with other palms. Among coryphoid palms, Rhapis may be considered intermediate in specialization. The connation in sepals and petals and corresponding derivation of sepal and petal traces in whorls are evidences of specialization, as is also the adnation of stamens and staminodes to the petal tube. Several features of the carpel are noteworthy. Completely free, stipitate, spirally inserted carpels are considered primitive in palms and angiosperms. However, the large dorsally extended styles and completely closed ventral sutures of Rhapis indicate specialization. The orientation of the ovule is intermediate between the primitive anatropous and the most advanced orthotropous position. The multiple derivation of traces to the ovule from the dorsal, several laterals, and a ventral carpellary bundle suggests laminar placentation (Eames, 1961) and may be a basic pattern in palms. In a preceding paper of this series it was stated that Rhapis has a relatively specialized inflorescence (Tomlinson & Zimmermann, 1968). Similarly it may be said that among the Coryphoideae the flowers are relatively specialized.

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GLYCOSMIS PENTAPHYLLA (RUTACEAE) AND RELATED INDIAN TAXA

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The publication of a new series, Limonia arborea, by Roxburgh (Pl. Coromandel. 1: 60. t. 85. 1798) and his providing the plant which he believed to be "Limonia pentaphylla Retz." (Roxb. loc. cit. t. 84) with a detailed description and illustration, as well as the subsequent discovery of the authentic type specimen of Limonia pentaphylla Retz. by Tanaka (Bot. Not. 1928: 156–160. 1928), has led to some controversy in the nomenclature of these two species now included in the genus Glycosmis. In the interest of clarity, relevant parts of the earlier works are reviewed in brief.

Tanaka (loc. cit.) pointed out that Limonia pentaphylla Retz. is conspecific with Limonia arborea Roxb. and is entirely different from the plant treated by Roxburgh as "Limonia pentaphylla Retz." He therefore treated Glycosmis arborea (Roxb.) Correa (= Limonia arborea Roxb.) as a synonym of Glycosmis pentaphylla (Retz.) Correa (= Limonia pentaphylla Retz.), and in Botaniska Notiser (1928: 159. 1928) proposed Glycosmis mauritiana (Lam.) Tanaka (= Limonia mauritiana Lam.) for the plant erroneously treated by Roxburgh as "Limonia pentaphylla Retz."

Narayanswami (Rec. Bot. Surv. India 14(2): 26, 1941) did not agree with Tanaka's view and maintained Limonia pentaphylla Retz. and Limonia arborea Roxb. as distinct from each other; accordingly the correct names in the genus Glycosmis should be G. pentaphylla (Retz.) Correa and G. arborea (Roxb.) Correa, respectively. Brizicky (Jour. Arnold Arb. 43: 88. 1962) upheld Tanaka's view on the conspecificity of Limonia pentaphylla Retz. and Limonia arborea Roxb. and remarked, "Narayanswami (1941), apparently having overlooked Tanaka's article on the type of Retzius' species, came to the conclusion . . . that Tanaka's interpretation of L. pentaphylla was entirely incorrect Brizicky also pointed out that De Candolle (Prodr. 1: 538. 1824), instead of Correa (Ann. Mus. Hist. Nat. Paris 6: 386. 1805), should be assigned the authorship of these two binomials, G. pentaphylla and G. arborea, since De Candolle made these combinations for the first time in the sense of the Code. However, Brizicky's conclusion on their nomenclature is untenable, not being in accordance with the existing Code. Brizicky (loc. cit., P. 87) is of the opinion that ". Glycosmis pentaphylla DC. was based on the plant identified and illustrated by Roxburgh as 'Limonia pentaphylla Retzius' and only questionably on Retzius' species

('G. pentaphylla, . . . Limonia pentaphylla Retz. obs. 5. p. 24? Roxb. cor. 1. t. 84.')." Brizicky (loc. cit., p. 89) further argues, "Then Glycosmis pentaphylla DC., based on Roxburgh's plant, not on that of Retzius, must be regarded not as a new combination, but as a new name in Glycosmis for the species for which Tanaka later (1928b) created the combination G. mauritiana (Lam.) Tanaka . . . Since G. pentaphylla DC. cannot be applied to Retzius' Limonia pentaphylla, the next available name for the latter species is Glycosmis arborea (Roxb.) DC." In treating Glycosmis pentaphylla as a new name and not as a new combination Brizicky was probably applying the provisions of Art. 72. However, this article is not operative in this case; it is clear from Roxburgh's treatment of "Limonia pentaphylla Retz." that he was not describing a new species under a homonymous name, but was only misidentifying Retzius' plant. Thus, the question of De Candolle's basing the binomial G. pentaphylla on "Roxburgh's plant — Limonia pentaphylla" does not arise. Moreover, De Candolle, in making the transfer (Prodr. 1: 538, 1824), gave a direct reference to Retzius' plant, though with a question mark, ".... Limonia pentaphylla Retz. obs. 5. p. 24? Roxb. cor. l. t. 84." It is evident from above that De Candolle was not certain about the identity of the two plants involved in the confusion. Hence, Brizicky's argument for treating the binomial Glycosmis pentaphylla as a new name cannot be accepted. Article 55 (par. 2) of the International Code of Botanical Nomenclature (ed. 1966) clearly states, "When, on transference to another genus, the specific epithet has been applied erroneously in its new position to a different species, the new combination must be retained for the species

¹Dr. Brizicky, who died on June 15, 1968, saw an earlier but hardly different version of this paper and, on May 4, 1968, set down the comments which follow. These comments were duly communicated to the authors of this paper, who are

still not agreeable to the arguments placed by Dr. Brizicky. "The authors of this paper believe that my view of Glycosmis pentaphylla DC. as a new name, rather than combination, is untenable from the standpoint of the Code, so they regard G. pentaphylla DC. as a new combination based on Limonia pentaphylla Retzius. They find evidence for this in the fact that 'De Candolle, while making transfer, gave a direct reference to Retzius' plant, "Limonia pentaphylla Retz. Obs. 5. p. 24?. . "' Curiously, though, applying the Code mechanically [Art. 55?], the authors disregard the question mark which follows the complete citation of Retzius' specific name and which expresses De Candolle's doubt of the conspecificity of Retzius' species with Glycosmis pentaphylla. This expression of taxonomic doubt indicates rather clearly that De Candolle could not and did not base his G. pentaphylla either nomenclaturally on Retzius' binomial or taxonomically on Retzius' species, which he knew only from a brief description, and that he questioned its conspecificity with G. pentaphylla. There seems to be no article in the Code directly referable to this situation, but, how can a serious botanist deliberately publish a new combination based nomenclaturally on one and taxonomically on another, supposedly different, species? Least of all can such a combination be expected from one of the founders of the rules of botanical nomenclature.

"Although neither prescribed nor required by the Code, the knowledge of the taxon which is being transferred and an at least reasonable certainty that the taxon, the epithet of which is used as basionym, is really identical or conspecific (convarietal, congeneric, etc.) with that for which a new combination is made, are a priori presumed to be possessed by a taxonomist who publishes a new combination, new status,